Mechanical tissue development in certain North American vines*

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During the year 1912, a study was made of various woody vines growing in temperate North America, with the idea that there might be some relation between them and intermediate forms bearing on the origin of the liana habit in these temperate regions. This paper refers more particularly to the mechanical tissues of these plants.

The liana habit of course shows no phylogenetic connections and in this respect is analogous to parasitism, saprophytism, etc. The habit evidently did not arise early in the temperate zone since among the plants indigenous to this zone it is developed to a very slight extent among the lower orders, Liliales perhaps being one of the first, that is, on the arbitrary basis of the coördination of structure with time of origin. In the tropics, however, the monocotyledonous families having the liana habit are much more numerous, e. g., some bamboos and various members of the Palmaceae, Pandanaceae, and Araceae, etc. But if, as some recent investigators (see Henslow, 5) conclude, the monocotyls arose from the dicotyls, this theory of chronological origin may be discredited altogether. At any rate, it is fair to suppose that the habit did not arise until there was such dense vegetation as to make the habit an advantage to the plant. Most of the lianas, according to Schenck's estimate (see Schimper, 7, p. 197) ten elevenths, are tropical because the conditions in the tropical rain forests are the causative factors, i. e., deficiency of light and abundance of moisture.

However, the simplest internal physiological reason for the origin of this vine habit seems to be the lack of adequate mechanical tissues. A secondary factor is the lengthening of the internodes but this is due to the evident physiological process of elongation by diffuse light reaction. This can easily be accounted for by an

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adaptive line of reasoning since the vine habit is most prevalent in habitats of diffuse light and plenty of water. As Schimper (7, p. 309) says, the origin of both lianas and epiphytes is to be traced to a low intensity of light and an abundance of moisture. But the lack of adequate mechanical tissue is not well accounted for. To attempt to explain this it seems to be necessary to look at the plant characters from a genetic point of view. Clearly the amount of mechanical tissue is a unit character in a plant and any variation in this direction affects this character. In the course of the formation of the ancestral germs of plants showing this habit there must have occurred a dissociation of characters and this segregation of characters associated together in the normal ancestor gave rise to their present form; since Bateson (2) says segregation thus defines the units concerned in the constitutions of organisms and provides the clue by which an analysis of the complex heterogeneity of living forms may be begun. Right in the line of this investigation is the peculiar phenomenon observed by de Vries in his *Oenothera* cultures in the specific example of *Oenothera rubrinervis*, which has among other characters bast fibers with thin walls. According to de Vries's observations *O. rubrinervis* arose once in every thousand seedlings and twelve times in cultures not in the direct line of descent, i. e., from the pure *O. Lamarckiana* family. In this instance de Vries thinks that if the group of *rubrinervis* characters could be dissociated, then its compound nature would be disclosed. How the unit can cause the bast walls to become thin cannot be explained, but he insists that the habit of a species can be so much altered by mutation that during its whole life and in every organ it differs from its parent species (**8**). Now, just as this could happen in *Oenothera rubrinervis*, could there not be a similar segregation and recombination of different characters so as to cause a decrease in the mechanical tissue of any plant in a period of mutation?

With this question in mind an examination of the stems of various plants in diverse families found in the temperate zone was made to see if there was a warrantable deficiency in mechanical tissue development to account for the inability of these plants to stand erect. This group of plants was composed of the following: *Rhus Toxicodendron*, var. *radicans* (L.) Torr., *Psedera quinque-*

folia (L.) Greene, *Vitis vinifera* L., *Hedera Helix* L., *Akebia quinata* L., *Rosa polyantha* L., *Lycium halimifolium* Mill., *Wisteria frutescens* (L.) Poir., *Lonicera japonica* Thunb., *Tecoma radicans* (L.) DC., *Rubus occidentalis* L., and *Kerria japonica* L.

The *Lonicera* was first examined and, as de Bary (1, p. 532) observed, this plant has a simple arrangement of its tissues, producing one zone of bast fibers and one of soft bast each year. This inner zone is just on the inner boundary of the bast and the wood fibers are disseminated in the xylem in single radial rows. The arrangement of fibrous strands gives sufficient tensile strength but is not enough to permit the plant to stand upright. These bast strands are not close enough together to give adequate support in an upright position. Under the epidermis the cortical parenchyma is somewhat thickened but as a source of mechanical support this is almost negligible. The wood cambium consists of ordinary parenchyma. Inside the soft bast zone between it and the pith there is a parenchymatous tissue called by Strasburger *vascular parenchyma*. This may give some support, particularly under a tension. The vascular elements occupy the remaining space. In older stems of the *Lonicera* of course the secondary tissues give considerable stability to the stem, but the primary xylem of a first year stem is not nearly enough to enable the stem to maintain a perpendicular position.

The stem of the *Akebia* is angled and for each ridge there is a large vascular bundle, oval in cross section. The bundles fill most of the space in transverse section. The most important mechanical tissue is the bast, which forms a small cushion, four or five cells in thickness, on the outer edge of each bundle. The bast fibers are heavy and have very small lumina but they are deficient in number. The cortical parenchyma is assimilative in the *Akebia* and therefore has very thin walls. The primary xylem is not important from a mechanical standpoint in this plant; the conductive elements occupy 58.3 per cent, while the mechanical tissue occupies only 8.3 per cent of the transverse area, i. e., a ratio of 7 to 1. The bast cells in the *Akebia* are thicker than those of the *Lonicera* but the numerical proportion is smaller.

In *Hedera Helix* the most noticeable feature is the narrowness of the medullary rays, which are only one cell thick. The mechan-

ical tissues are represented only by the xylem and the small amount of bast next to the outer cortex parenchyma. A peculiar feature of this latter is that under certain conditions it is greatly increased and bush forms of the *Hedera* can be noted in many gardens. The occurrence of this form as a variety is frequently noted in botanical literature (see de Vries, **8**, vol. 1, p. 44). This would go to show that in the ivy, if it grows as a bush, i. e., if it is well fertilized and pruned, the bast elements will develop to such a degree that it can maintain an erect position. The shock of pruning seems to cause this undue development of bast. This plasticity of the stereome development offers ground for the theory that the liana habit arose from erect plants.

In the *Rhus* there are almost no medullary rays to be clearly distinguished, the primary xylem is well developed and in the phloem the resin ducts are seen, as mentioned by de Bary (**1**, p. 452). The mechanical tissues are poorly developed in primary growth except the collenchyma, of which there are approximately three layers of cells. In the secondary growth the bast fibers are parallel in development with the secondary wood. In the *Rhus* the estimate is 39.51 per cent for the vascular elements.

The *Wisteria* shows the greatest development of sclerenchymatous fibers with very heavy walls, so that they appear almost solid. In the wood cambium and the cortical parenchyma there are a great many calcium oxalate crystals and in the latter region are also many irregularly shaped stone cells. These give the plant considerable strength, but there are not enough of the long fibers to produce a solid cylinder. A young plant with this amount of mechanical tissue can keep an erect position until it is a half meter high, when the weight of the increasing growth becomes too great for these tissues and it assumes a recumbent position. This was observed in young plants grown under various conditions and in different situations. The leaning position is assumed much earlier in diffuse light.

There are peculiar conditions in the mechanical development of the *Lycium*. This plant is half shrub and half vine. Its manner of growth is most interestingly discussed by Kerner von Marilaun (**6**, vol. 1, p. 672). The xylem occupies a very large space and the bast is developed so as to fill 18 per cent of the transverse area.

The pith and the parenchyma of the cortex also occupy relatively large spaces and contribute nothing to support. In this plant the characteristics of the ivy are again reviewed. If the *Lycium* is grown in open situations, such as fields, the plants can make a growth of several meters before becoming entirely prostrate, and if pruned will form a dense, shiny shrub. If it grows in diffuse light near a support, however, the characteristic "leaner" habit or, as Kerner von Marilaun calls it, the "weaving" habit, is developed.

The *Psedera* has a very definite arrangement of the mechanical tissues. The xylem occupies almost a continuous cylinder outside the pith, the rays separating the bundles being very narrow. In the wood cambium the bast fibers conform to the type called by de Bary branched sclerenchymatous fibers, forming a continuous cylinder with a thickness of six cells. This makes the stems very tough and by experiment in the laboratory it was found that a stem of one season's growth, 70 cm. long and 0.3 cm. in diameter, bore a strain of 8845.2 grams before breaking but could not support an erect position in a stem of the same dimensions more than 70 cm. in length. These sclerenchymatous fibers in transverse action measured 0.06–0.08 mm. in their greater dimension and 0.01–0.02 mm. in the shorter, the sections being irregularly oblong; the lumina were about 7 μ wide, thus showing the walls to be comparatively heavy. According to the above experiment, however, the fibers do not suffice to maintain the stem in an upright position.

The arrangement in the *Vitis* is similar to the preceding in a great many respects. The xylem is here developed to a greater extent and this gives a considerable support. The medullary rays are clearly defined and also the cambium ring. In the *Tecoma* there is very good reason for the toughness of the stem. In transverse section, by measurement it was seen that in a belt of the cortical parenchyma 0.9 mm. wide there were thickly scattered groups of short sclerenchymatous fibers and also a heavy reinforcement in the external layer of collenchyma. The stem, too, occupies a large area. In fact, in the *Tecoma* the vascular elements occupy 33⅓ per cent of the stem and the secondary thickening is, of course, very interesting. Haberlandt (4, p. 629) remarks that Sanio first observed that the wood and bark formation took place in the reverse order from most plants.

However, as the secondary thickening is not considered in this study, its details will not be mentioned. A peculiar though common phenomenon is seen in the *Tecoma* in that there is a great increase in the parenchymatous tissues on the side from which adventitious roots or holdfasts are put out, so that there is a great differential growth seen in transverse section.

In the *Rosa*, which is a "leaner" or "weaver" according to Kerner von Marilaun's terminology, the vine habit is almost lost. This is like the *Hedera* inasmuch as it has so much plasticity that by proper culture it can be made to assume a tree-like or shrub-like form. The mechanical tissues are well represented, the large, thick-walled fibers form an interrupted sheath in the transverse section and there are also many large crystals of calcium oxalate in the peripheral region; the collenchyma is very thick-walled and the xylem is arranged in numerous narrow bundles separated by frequent, though attenuated medullary rays. The *Rubus* shows very similar characters. This genus is also included in Kerner von Marilaun's weaving category, but it has various species in southern Asia and Australia which are typical lianas. In both *Rosa* and *Rubus*, of course, the pith area is very large in cross section. In the *Rubus* the bast fibers form a heavy belt and the collenchyma too is developed to six layers of cells. The last species studied, *Kerria japonica*, is a weak shrub and never develops any vine habit. In this plant, however, the mechanical support does not seem to come so much from the bast fibers, etc., as from the principle of construction, i. e., a very firm outer cylinder filled with pith. The bast fibers are large but few in number and scattered in small groups, the perennial epidermis doubtless also contributing to the stability of the stem as also the lignified tissues of the very broad, flattish vascular bundles.

Now in looking over the anatomy of this group of plants it would seem that the variation in stereome elements in stems would naturally be a factor of great importance in the evolution of the vine habit. Of course the first and most important agent is light, since light by its action on the chloroplast tends to change the shape of the cell. Diffuse light is known to cause an elongation of parenchymatous cells and this of course produces elongation in an organ. This then partially accounts for the elongated habit of

vines but why there should be also a decrease in the mechanical tissues or at least an inefficiency in support for the stem can not be explained on this basis. The fact that reduced photosynthesis due to shade can bring about a decrease in constructive tissues might seem of some importance, but plants that have the habit develop characteristically in full light as well as shade so this argument is negligible.

So it would seem that there must be some basis for argument in support of the position taken before, viz., that in the light of de Vries's classic experiment on *Oenothera* the mechanical tissue development has its origin in the unit characters of the plant. As these are partially dependent on nutriment in the ancestors it follows that there must have been considerable variation in the premutation stages of the vines studied. As de Vries says all mutations are not progressive, i. e., visibly differentiated, we may speculate and suppose the plant to have undergone a retrogressive mutation which produces a change, a decrease in the bast fibers, etc. These characters then of the normal type have become latent or suppressed and may be retained as internal units, e. g., in the *Hedera* and at a future time under proper conditions may become activated. When once the plant has become a "leaner" by deficiency in mechanical support the secondary result of diffuse light can produce its effects towards elongation. However, this is speculation and mere argument based on *a posteriori* grounds. As stated above, all mutations need not be advantageous, and the first stages in the vine habit may have been distinctly disadvantageous. It may be said that the primary variation in mechanical tissues is due to recombination of the characters of certain plants and that plants with vine habits arise as mutations due to the preceding causes. In conclusion a quotation from the Chicago Textbook (**3**, p. 656) may give the general idea of this line of evolution: "It is assumed, and probably correctly, that lianas have come from erect ancestors, and that their evolution was subsequent to that of trees. . . . Probably the first lianas were leaners, the twiners and tendril climbers developing later."

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